

# American Museum Novitates

---

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY  
CENTRAL PARK WEST AT 79TH STREET, NEW YORK 24, N.Y.

---

NUMBER 1850

NOVEMBER 8, 1957

---

## A Fossil Collection from Northern Venezuela 1. Toxodontidae (Mammalia, Notoungulata)

BY RICHARD VAN FRANK<sup>1</sup>

### INTRODUCTION

The present paper is the first part of a report on a collection of fossils made by George Gaylord Simpson in 1938 and 1939 in northwestern Venezuela. Dr. and Mrs. Simpson, at the invitation of the Venezuelan Government, which generously defrayed the field expenses, spent the time from September, 1938, to May, 1939, in collecting the material to be described. They were assisted in the field by various people from near-by settlements.

The collection consists chiefly of remains of giant ground sloths (*Eremotherium rusconii* [Schaub]), and contains also the following: scant remains of a smaller ground sloth; glyptodont scutes; horse teeth; a gastropod (*Eudolochotis distorta* Bruguière); and at least two kinds of toxodontids, herein described. All the mammals are Pleistocene of unknown precise age. In addition, younger beds have yielded a few fragments of a deer (*Odocoileus* sp.) and some gastropods (*Aperostoma venezuelense* Bartsch and Morrison). Both species of snails are still extant in the region, as I am informed by Dr. Joseph Bequaert of the Museum of Comparative Zoölogy, who very kindly identified them and said that they often burrow deep during hibernation, which makes it difficult to know whether or not they are as old as the containing matrix.

The non-toxodontid remains will be dealt with in the second, final, part of the report.

---

<sup>1</sup> Museum of Comparative Zoölogy, Cambridge, Massachusetts.

All the fossils were found near the small town of San Miguel, on the eastern edge of the district of Giménez, state of Lara, about 35 kilometers southwest of Barquisimeto (fig. 1). The Quaternary beds in the San Miguel region are mainly stream-terrace deposits underlain by Cretaceous. "The Pleistocene beds everywhere in this area are remnants of the filling of a still older but also essentially similar system of *zanjones* [arroyos]. . . . The Pleistocene beds . . . show poor sorting and a mixture of pebbles from the Cretaceous country rock with clay which evidently is decomposed Cretaceous shale" (Simpson, MS). Two quarries near San Miguel (fig. 2) are the chief source of the fossils, most of which, however, were found as surface drift. One of the quarries is in the *Zanjón del Murciélago*, which lies about 3 kilometers south and west of San Miguel. This *zanjón* "trends more or less North of East, descends from the saddle immediately north of Cerro del Ánima, to the Rio Turbio on the Hacienda San Gerónimo. Total length ca. 1½ km." (Simpson, MS). The absolute elevation is about 960 meters. The fossils were found in a bone bed about 160 cm. thick and 6 meters above the *zanjón* bottom, characterized by "Greenish clay with many pebbles, grading with heavy, ill-sorted or greenish conglomerate with many bones" (Simpson, MS). The second quarry is about 450 meters south of San Miguel, at an absolute elevation of 1010 meters. The lithology is essentially the same as at the first. Bones were found also in nearly all the *zanjones* shown in the map (fig. 2).

The bones are usually fragmented, surrounded with a hard, limy crust, and heavily mineralized; none are definitely associated. The surface color of most is a mixture of mottled black and gray, with the interior a lighter gray; a few are light brown. Most of the teeth have black dentine and light gray enamel; a few have cream-colored dentine protected by dense, adhering matrix. Several have light tan enamel and darker dentine.

The following abbreviations of the names of institutions are used:

A.M.N.H., the American Museum of Natural History

A.N.S.P., Academy of Natural Sciences of Philadelphia

C.L.S., Colegio La Salle, Barquisimeto, Venezuela

C.N.H.M., Chicago Natural History Museum

D.G.M., Divisão de Geologia e Mineralogia do Departamento Nacional da Produção Mineral, Museu Nacional, Rio de Janeiro, Brazil

M.C.Z., Museum of Comparative Zoölogy, Harvard University

U.C.M.P., University of California (Berkeley) Museum of Paleontology

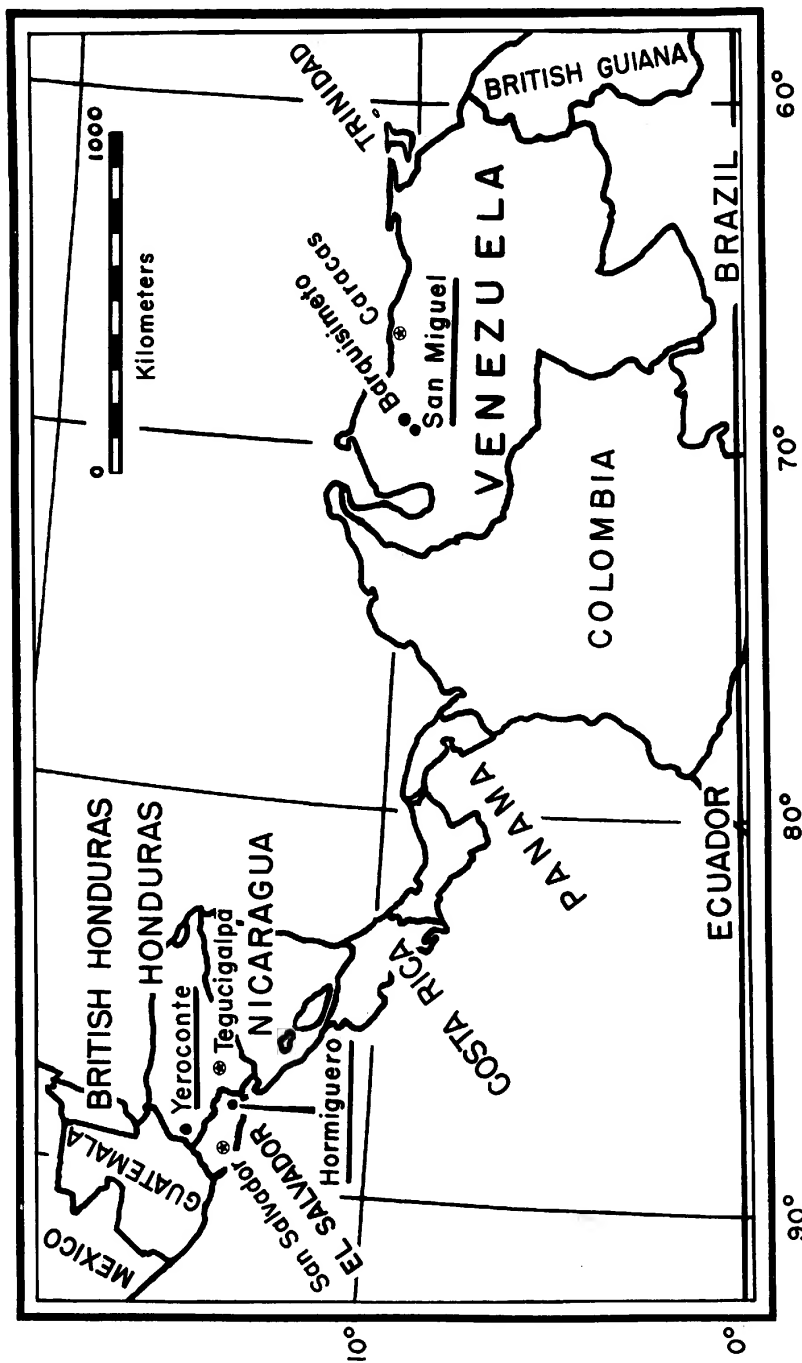


FIG. 1. Simplified map of Central America and northern South America. Names of fossil localities underlined.

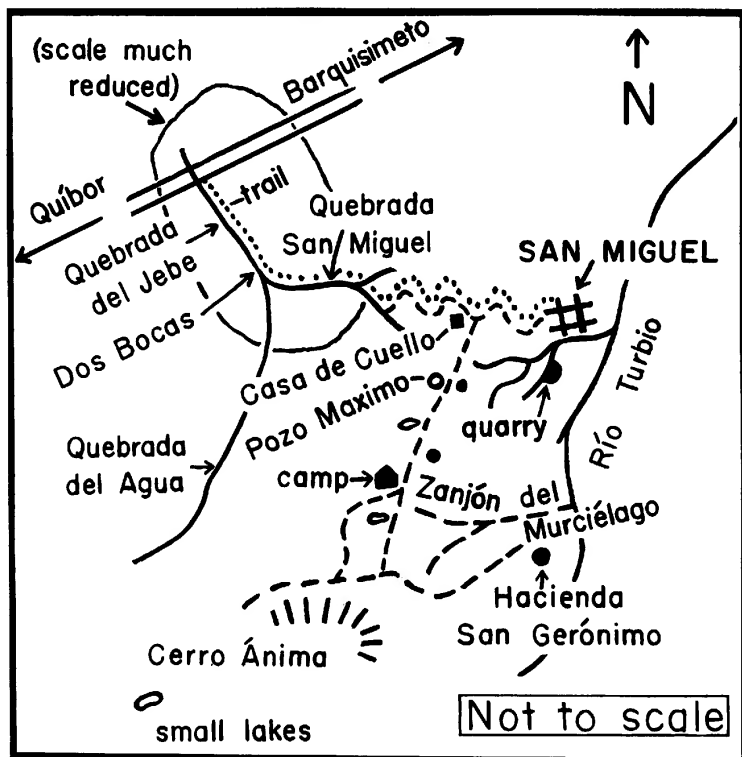


FIG. 2. Sketch map of the area around the San Miguel fossil locality, Giménez, Lara, Venezuela, 1938–1939. Not to scale.

In the tables and other measurements, a question mark (?) signifies a measurement that is inaccurate because of poor state of preservation.

#### TOXODONTID MATERIAL

The San Miguel toxodontid material is catalogued in the American Museum of Natural History, Department of Geology and Paleontology, and consists of five lower jaw fragments, a number of isolated teeth, one axis, one radius, five ulnae, one patella, and one calcaneum. All seem to be from adults.

All the lower jaws are doubtless from the same species. The two largest pieces (A.M.N.H. Nos. 48851, left, and 48852, right) are probably from the same individual, and overlap A.M.N.H. No. 48854, a symphyseal portion, through  $P_3$  and  $P_4$ . These three specimens together present the complete lower dentition. Many of the isolated teeth are

definitely, some are probably, and a few are definitely not, assignable to the species represented by the major jaw fragments.

The only genera that need be seriously considered in connection with the San Miguel lower jaws are *Gyrinodon* Hopwood, *Neotrigodon* Spillmann, *Stereotoxodon* Ameghino, *Toxodontherium* Ameghino (*T. imbricatum* Nectario Maria was described from a near-by locality), and *Trigodonops* Kraglievich. But the San Miguel form, it seems to me, could not be included in any of the above genera without their drastic redefinition. The various characters that are considered below in the determination of the relationships of the San Miguel species may or may not prove valid when the family is better known phylogenetically and morphologically. But by such characters toxodontid genera are now distinguished, and therefore, at least until the family is more nearly understood, I believe it necessary to describe a new genus for the San Miguel species.

As to subfamilial affinities, it is clear only that we are not dealing with a nesodontine. Beyond that I can see only dilemma. In a commonly used classification of the Toxodontidae the non-nesodontine genera are divided into two other subfamilies: Toxodontinae ( $M_{1-2}$  with meta-entoconid and ento-hypoconid folds<sup>1</sup>; at least one upper premolar—i.e.,  $P^4$ —with a lingual enamel fold;  $M^{1-2}$  with a metaloph) and Haplodontheriinae ( $M_{1-3}$  without meta-entoconid fold;  $P^{1-4}$  without a lingual fold;  $M^{1-3}$  without a metaloph). Pascual (1954), however, suggests that the taxon containing *Xotodon* Ameghino and closely related genera should perhaps be revived as a subfamily. In any case, the San Miguel genus does not fit into any subfamily thus far defined, as  $M_1$  has the meta-entoconid fold present and well developed, while  $M_2$  has it weak or absent. Some of the San Miguel upper cheek teeth, however, are at least descriptively toxodontine. It was at first impossible to decide whether these upper teeth went with the lower jaws in the same species, because the collection contains two isolated  $I_3$ 's that are very different from those in the jaws. Fortunately I have had the privilege of seeing the toxodontid material collected by Drs. Paul O. McGrew and Albert A. Potter in Honduras (McGrew, 1942), which includes an incisor practically identical with the  $I_3$  of the San Miguel jaw, and two upper premolars (probably a pair) associated with the incisor and practically identical with A.M.N.H. No. 488641 from San Miguel, pre-

---

<sup>1</sup> See figures 8A and 10 for these and other dental terms, which are intended for reference primarily, some of the homologies being doubtful.

sumed to be a P<sup>4</sup>. These P<sup>4</sup>'s are descriptively toxodontine. In default of evidence to the contrary, I consider it reasonable to associate No. 48864 l with the lower jaws in the same species.

I propose the name *Mixotoxodon* for the new genus, as the lower dentition mixes characters of two subfamilies. This is the sort of thing that occurs in *Ocnerotherium* Pascual (1954), from the Miocene of San Luis, Argentina, suggested in the specific name *intermedium*. Pascual placed this in the Toxodontinae because he felt that the toxodontine lower and upper molars outweighed the haplodontheriine upper premolars in taxonomic importance. I follow this precedent and place *Mixotoxodon* in the Toxodontinae, but question whether the distinction between Toxodontinae and Haplodontheriinae is really valid. In fact, a new Santacrucian toxodontid now under study by Patterson and van Frank (MS), which displays still another unique combination of characters, will doubtless put an end to that subfamily distinction—whatever the xotodonts may turn out to be.

FAMILY TOXODONTIDAE  
SUBFAMILY TOXODONTINAE  
**MIXOTOXODON**, NEW GENUS

GENOTYPE: *Mixotoxodon larensis*, new species.

DIAGNOSIS: Sides of symphyseal portion of lower jaws not divergent anteriorly. Lower incisors positioned so as to form a labially convex hemicylinder; projecting relatively less from the alveoli than in *Toxodon*. Cross section of I<sub>1-2</sub> a triangle with the greatest dimension vertical; enamel confined to labial surface and to a narrow strip on lingual surface. I<sub>3</sub> similar but with greatest dimension horizontal; angles more rounded. All premolars without enamel on lingual side. Meta-entoconid fold deep in M<sub>1</sub>; weak or absent in M<sub>2</sub>.

RANGE: Northern South America and Central America; Pleistocene.

**Mixotoxodon larensis**, new species

HOLOTYPE: A.M.N.H. No. 48854, symphyseal portion of lower jaws with left I<sub>1-2</sub>, right I<sub>1</sub>-P<sub>3</sub>, most P<sub>4</sub>.

PARATYPES: A.M.N.H. No. 48851, most of left lower jaw posterior to P<sub>4</sub>, with M<sub>1-3</sub>. A.M.N.H. No. 48852, part of right lower jaw with part of P<sub>3</sub>, and with P<sub>4</sub>-M<sub>3</sub> (probably from same individual as No. 48851). Fragments of lower jaws, A.M.N.H. Nos. 48853 (left) and 48855 (right), both with M<sub>2-3</sub>. Isolated teeth: A.M.N.H. Nos. 48858, 48862a, 48864b, all P<sub>4</sub>; No. 48860b, M<sub>1</sub> fragment; Nos. 48864e, 48864a, both M<sub>2</sub>. C.N.H.M. No. P-26969, right I<sub>3</sub>. U.C.M.P. No. V4201/37040, left M<sub>2</sub>.

REFERRED TEETH: A.M.N.H. Nos. 48864c and 48866, both probably  $P_4$ ; No. 48864 l, upper premolar, probably  $P^4$ . C.N.H.M. Nos. P-26963 and P-26964, right and left upper premolars (probably a pair), same tooth as A.M.N.H. No. 48864 l ( $P^4$ ?); C.N.H.M. No. P-26965, upper molar fragment.

LOCALITIES: American Museum material from near San Miguel, Lara, Venezuela, about 35 kilometers southwest of Barquisimeto. A.M.N.H. No. 48866 from Zanjón del Murciélago, about 3 kilometers southwest of San Miguel; all the rest from the quarry about 450 meters south of San Miguel. Chicago Natural History Museum material: Yeroconte, province of Copan, Honduras, near Dolores de Copan (McGrew, 1942). University of California material: Hormiguero, department of San Miguel, El Salvador (Stirton and Gealey, 1949, p. 1751, fig. 4C).

HORIZON: Pleistocene, precise age unknown. The Honduras and El Salvador specimens are from bog deposits, surely late Pleistocene and probably very late.

DIAGNOSIS: As for the genus.

DESCRIPTION: *Mixotoxodon larensis* is comparable in size to *Toxodon platensis* Owen.

The symphyseal portion of the mandibles (figs. 3, 4A, 5A; table 1) is badly broken, particularly on the left side, which makes it impossible to see whether the sides anterior to  $P_2$  are parallel or convergent anteriorly. In any case they are not divergent. *Mixotoxodon larensis* shares with *Toxodon* the distinction of having no "chin," as the incisors are quite procumbent. The symphysis is completely fused, leaving no trace of the suture. It extends posterior to  $P_4$  in the type specimen (fig. 3A), probably to the middle of  $M_1$ . In A.M.N.H. No. 48851 it extends no farther back than to the anterior border of  $M_1$ . There is a large mental foramen adjacent to the anterior two-thirds of  $M_1$ , a somewhat posterior position. The mandibular foramen is a vertically elongated slot about 7 cm. high and opening like a trouser pocket. The sigmoid notch seems to be shallow relative to the situation in *Toxodon*.

So far as can be seen, all the teeth are open-rooted and increase in cross section towards the root. There is no trace of cement on any of them. Nearly all the teeth in the collection have on the surface of the enamel very fine grooves and ridges, fairly evenly spaced, and barely visible to the naked eye as parallel, transverse striations. They vary in number from about 25 to 75 per centimeter in different specimens. In addition, most of the teeth have much coarser longitudinal grooves of varying depth, width, and distance apart.

TABLE 1  
MEASUREMENTS (IN MILLIMETERS) OF LOWER JAWS OF *Mixotoxodon larensis*

	A.M.N.H. No. 48851	A.M.N.H. No. 48854	A.M.N.H. No. 48855
Length of symphysis	—	177	—
Width at center of P <sub>1</sub>	—	90?	—
Width at center of P <sub>4</sub>	—	125?	—
Depth at center of M <sub>3</sub> , lingual side	154	—	ca. 160
Maximum thickness at center of M <sub>3</sub>	55? <sup>a</sup>	—	50?
Depth at coronoid process	335	—	—

<sup>a</sup> Also in A.M.N.H. No. 48852.

The incisors in the lower jaws are crowded together at their free ends (figs. 3, 4A, 5A; table 2). The wear facets of I<sub>1-2</sub> are only slightly less than 90 degrees to the horizontal plane of the teeth at the ventral border, so that the wear is confined virtually to the anterior end (figs. 3B, 4A). I<sub>3</sub> is worn obliquely on the lateral side in both the type and the Honduras specimen, although somewhat more in the former (cf. figs. 3B, 10E). The Honduras specimen is less convex labially and has a slight concavity in cross section in the ventromedial surface, whereas the San Miguel I<sub>3</sub> is convex here (cf. fig. 7A, B). Other than in these minor features, the two teeth scarcely differ.

The next tooth (figs. 3A, 7A; table 3), here called P<sub>1</sub> as a little more likely than canine, presents no evidence of ever having had enamel, but it must be noted that more than two-thirds is missing. There is less space between P<sub>1</sub> and P<sub>2</sub> than between any two of the other premolars.

P<sub>2</sub> (figs. 3B, 4A, 5A, 7A; table 3) is slightly retrorse and introverted—more curved than any of the other lower cheek teeth.

The longitudinal labial groove in P<sub>3</sub> (figs. 3B, 4A, 7A; table 3) divides the tooth into two approximately equal halves, the trigonid and the talonid. This groove is shallow compared with that of P<sub>4</sub>. Only the talonid of the P<sub>3</sub> is preserved in A.M.N.H. No. 48852; it is similar to that of the type.

P<sub>4</sub> (table 3) is variable from specimen to specimen. The labial fold is a deep sulcus that reaches almost to the middle of the tooth (figs. 3, 4A, 7A), except in A.M.N.H. No. 48864b, in which it is almost as shallow as in P<sub>3</sub>. The trigonid is relatively longer (with respect to the talo-



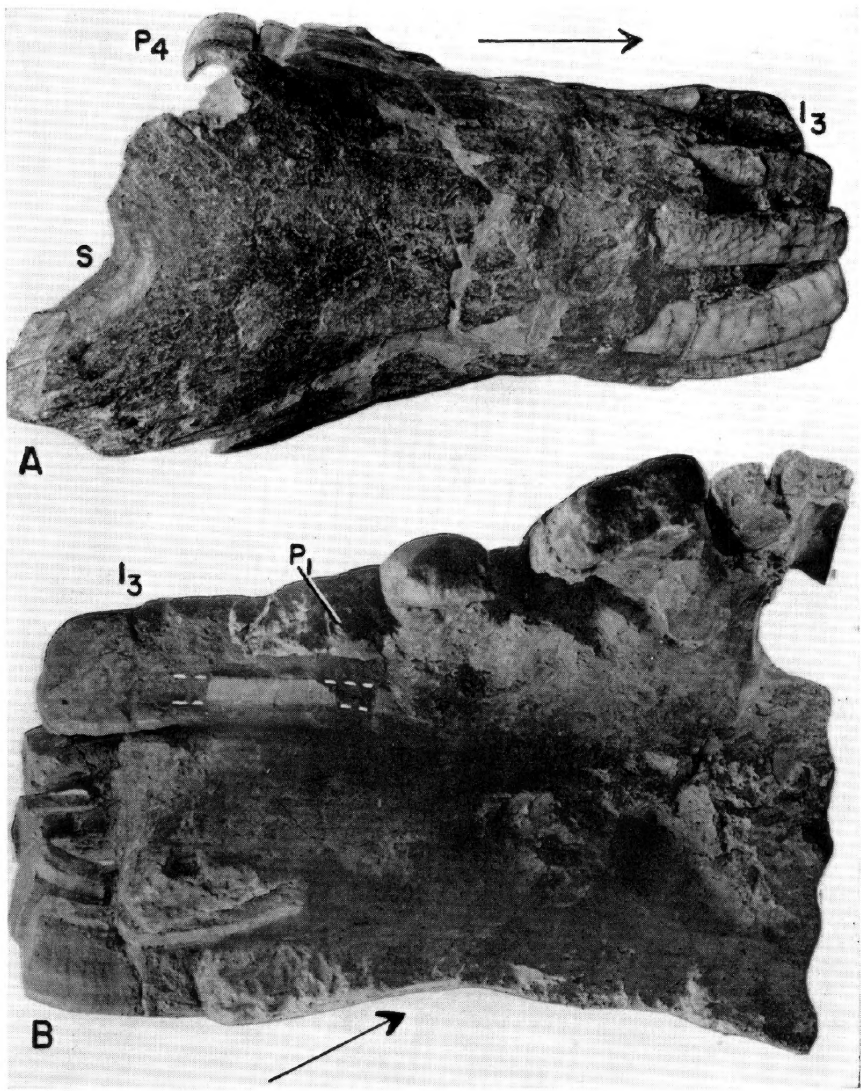


FIG. 3. *Mixotoxodon larensis*, new genus and species, holotype, A.M.N.H. No. 48854, symphyseal portion of mandibles. A. Ventral view, right side turned slightly out.  $\times 2/5$ . B. Dorsal view, left side raised slightly up.  $\times 3/5$ . Abbreviation: S, posterior end of symphysis. The arrows indicate the direction of illumination.



FIG. 4. A. *Mixotoxodon laevis*, montage of left mandible, lateral view. Symphyseal portion reversed from right side of holotype, A.M.N.H. No. 48854; remaining part, paratype, A.M.N.H. No. 48851.  $\times 1/4$ . B. Cast of right  $I_2$  of Nicaraguan toxodontid, described by Leidy as  $I_2$ , A.N.S.P. No. 12110, lingual view, anterior end raised about 45 degrees.  $\times 3/8$ .

TABLE 2

MEASUREMENTS<sup>a</sup> (IN MILLIMETERS) OF LOWER INCISORS OF *Mixotoxodon larensis*

	Width	Depth	Width of Lingual Enamel Band
A.M.N.H. No. 48854			
I <sub>1</sub>	16	23?	2.5
I <sub>2</sub>	15?	22?	2
I <sub>3</sub>	ca. 27	13?	5
C.N.H.M. No. P-26969, I <sub>3</sub>	14?	16	7

<sup>a</sup> All teeth were measured in a transverse plane just proximal to the attrition surface. Length along the main axis of tooth growth is not recorded in the tables.

nid) in the type than in the other specimens. Details of curvature and wear differ. A.M.N.H. No. 48862a is slightly concave vertically in its anterior face, convex posteriorly; the other P<sub>4</sub>'s are either nearly straight or perhaps a little curved the other way. A.M.N.H. Nos. 48858 and 48864b are more strongly introverted than the other P<sub>4</sub>'s—almost as much as P<sub>2</sub> of the type specimen. In A.M.N.H. No. 48862a the trigonid extends about 2.5 cm. higher than the talonid and rises to a sharp point anteriorly, a most unusual sort of wear, indicating, perhaps, a broken tooth above. A.M.N.H. Nos. 48864c and 48866 have the wear mainly on the labial side; a broad V notch in A.M.N.H. No. 48866 is gouged out of the entire labial border of the talonid, as if with a corner chisel. The animal that had this tooth must have had a considerable overbite on this side. The other P<sub>4</sub>'s have lost most or all of the biting surface during fossilization. Isolated premolar fragments A.M.N.H. Nos. 48864c and 48866 are probably P<sub>4</sub> (the trigonid is shorter than the talonid), but the trigonid is rounded instead of squarish, and the labial sulcus is shallow: in A.M.N.H. No. 48864c slightly more, in A.M.N.H. No. 48866 slightly less, than in A.M.N.H. No. 48864b. The biting surface slopes forward and upward in No. 48866, forward and downward in No. 48864c. None of the premolars have lingual enamel, although all but P<sub>1</sub> have a definite lingual groove between the trigonid and talonid. According to Roth (1898, p. 69) in *Toxodon* the lingual enamel band of the last two premolars disappears with age. I presume, however, that the groove disappears too.

M<sub>1</sub> is one of the most extraordinary toxodontid teeth I have ever seen (figs. 5B, 8A; table 4). The lingual surface of the metaconid, in

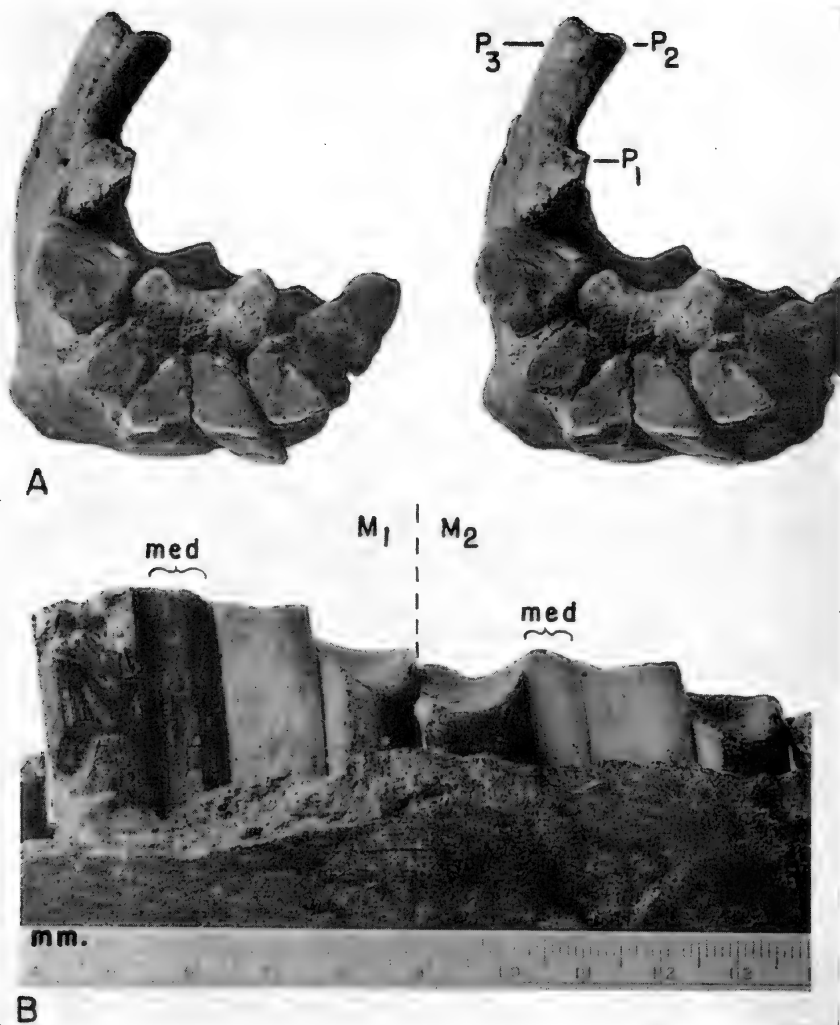


FIG. 5. *Mixotoxodon larensis*. A. Holotype, A.M.N.H. No. 48854, stereograph of mandibles, anterior view.  $\times 1/2$ . B. Portion of paratype, A.M.N.H. No. 48852, showing right  $M_{1-2}$ , lingual view.  $\times 1$ .

contrast with the case in every other toxodontid lower molar known to me, is entirely devoid of enamel. I have exposed nearly the whole lingual side of the tooth in both specimens and find that while the enamel is involved with the meta-entoconid fold in the usual way, it quite fails to extend anterior to the entoconid. Whether this most unusual feature is characteristic of the species or is an individual abnormality

TABLE 3  
MEASUREMENTS (IN MILLIMETERS) OF LOWER PREMOLARS OF  
*Mixotoxodon larensis*

	Total length <sup>a</sup>	Trigonid <sup>b</sup> Length by Width	Maximum Width of Talonid
A.M.N.H. No. 48854			
P <sub>1</sub>	10 <sup>c</sup>	—	—
P <sub>2</sub>	16.5?	9×11.5	11?
P <sub>3</sub>	26.5	12×13	15?
P <sub>4</sub>	31?	13?×18	—
A.M.N.H. No. 48852			
P <sub>3</sub>	—	—	16?
P <sub>4</sub>	32?	13×17	20
A.M.N.H. No. 48858, P <sub>4</sub>	32.5	12?—	—
A.M.N.H. No. 48862a, P <sub>4</sub>	ca. 33	13?×18	20
A.M.N.H. No. 48864b, P <sub>4</sub>	31.5	13.5×15	18
A.M.N.H. No. 48864c, P <sub>4</sub> ?	29	12×14	16
A.M.N.H. No. 48866, P <sub>4</sub> ?	30	13.5×15	18

<sup>a</sup> Measured from anterior to posterior end of enamel band.

<sup>b</sup> Length measured from anterior end of enamel band to medial end of labial enamel fold.

<sup>c</sup> Width, 10.

cannot now be determined, and is therefore not included in the diagnosis. The fragment (A.M.N.H. No. 48860b) is a posterior half of a right tooth broken off cleanly at the metaconid; the crucial part is missing. It is a little more convex labially and posteriorly than the other specimens and has a very shallow, gentle concavity (like a vertical trough) in the labial side centered opposite the ento-hypoconid fold.

M<sub>2</sub> is a very variable tooth (table 4). The meta-entoconid fold is absent as such in A.M.N.H. Nos. 48851 and 48852, but is represented by a vertical trough. It is present but only 1.5 to 2 mm. deep in the smaller jaw fragments (Nos. 48853 and 48855), and in isolated specimen A.M.N.H. No. 48864a (fig. 6A); it is still deeper in isolated specimen A.M.N.H. No. 48864e. The trigonid is about 2 mm. wider than the talonid in Nos. 48851 and 48852; about 0.7 mm. wider in No. 48864a; about 0.5 mm. narrower in No. 48864e. The El Salvador specimen (fig. 8B) has, relatively, the widest trigonid (exceeding the talonid by about 3 mm); otherwise it is proportioned almost exactly as in

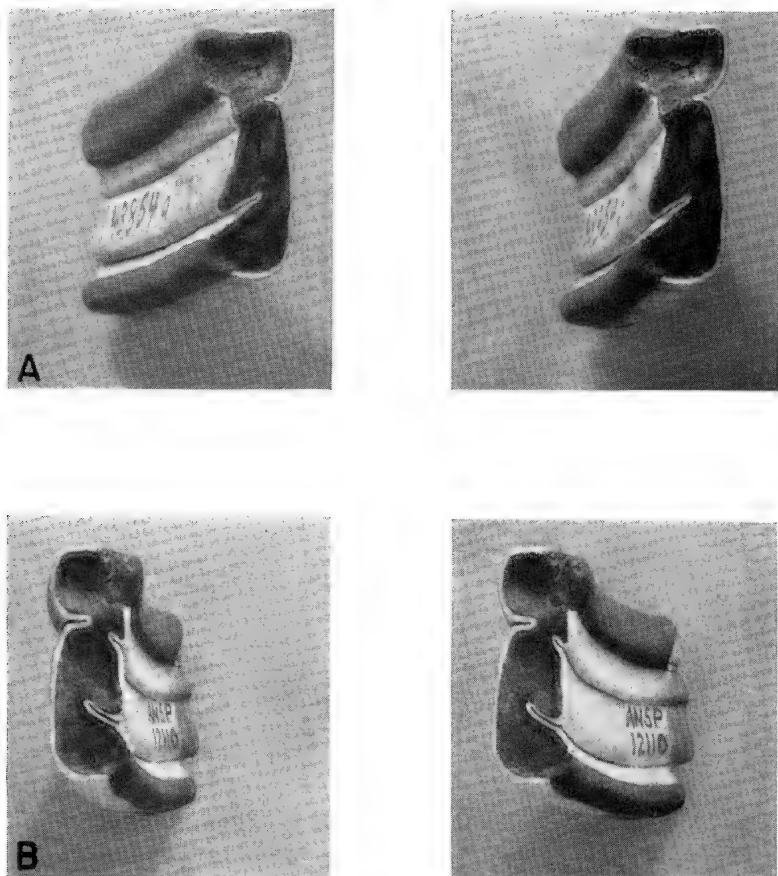


FIG. 6. A. *Mixotoxodon larensis*, stereograph of isolated right  $M_2$ , paratype, A.M.N.H. No. 48864a. B. Stereograph of left  $M_2$  of Nicaraguan toxodontid, described by Leidy, A.N.S.P. No. 12110. In both specimens enamel has been touched up with white, dentine with black. Both  $\times 2/3$ .

A.M.N.H. No. 48864a. The metaconid is relatively short in Nos. 48864e and 48864a. The lingual face of the trigonid is wholly convex in all specimens except A.M.N.H. Nos. 48864e and 48864a and the El Salvador specimen, which have a shallow concavity opposite the ento-hypoconid fold.

$M_3$  is well preserved only in jaw No. 48851 (figs. 4A, 8A; table 4). The specimens in the other three jaws have no noticeable peculiarity not ascribable to age and/or state of preservation. This tooth lacks the ento-hypoconid fold, and, as in other toxodontids, its axis of growth is

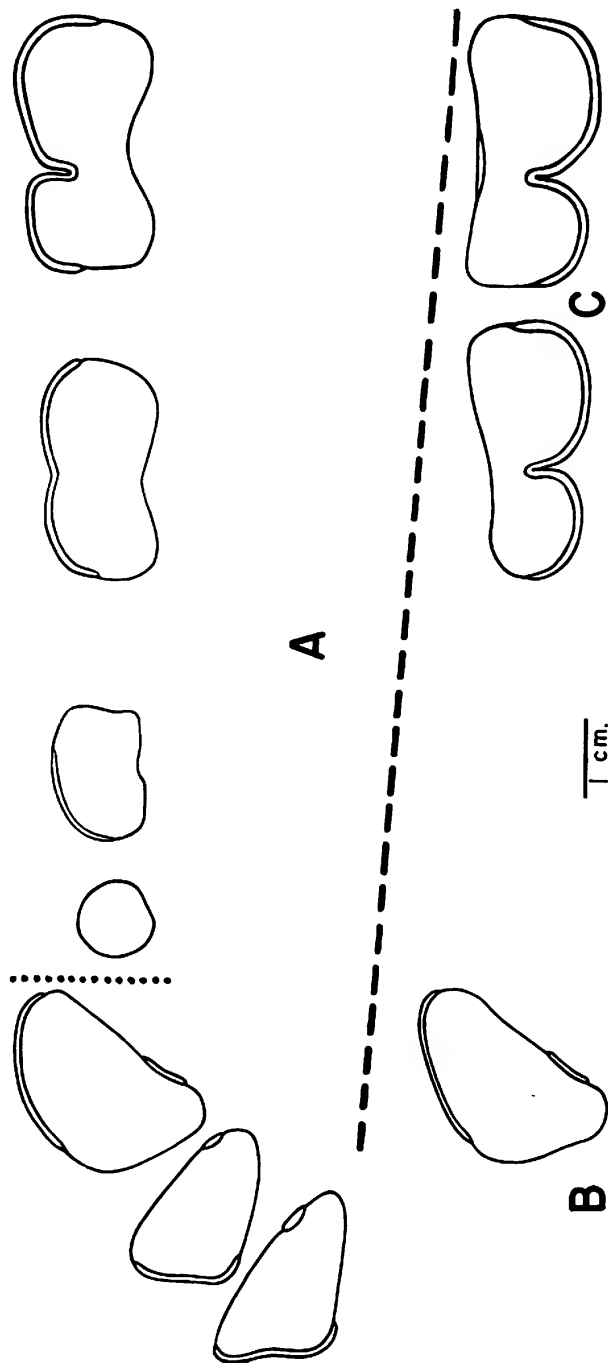


FIG. 7. A. *Mixotoxodon larensis*, holotype, A.M.N.H. No. 48854, right I<sub>1</sub>-P<sub>4</sub> (I<sub>1-2</sub> reversed from left side). The dashed line represents the symphysis. B. *M. larensis*, Honduras specimen, C.N.H.M. No. P-26969, right I<sub>3</sub>. C. *Trigodonops lopesi* (Roxo), holotype, D.G.M. No. 55-M, left P<sub>3-4</sub>. All figures in crown view of cross section; all  $\times 1$ .

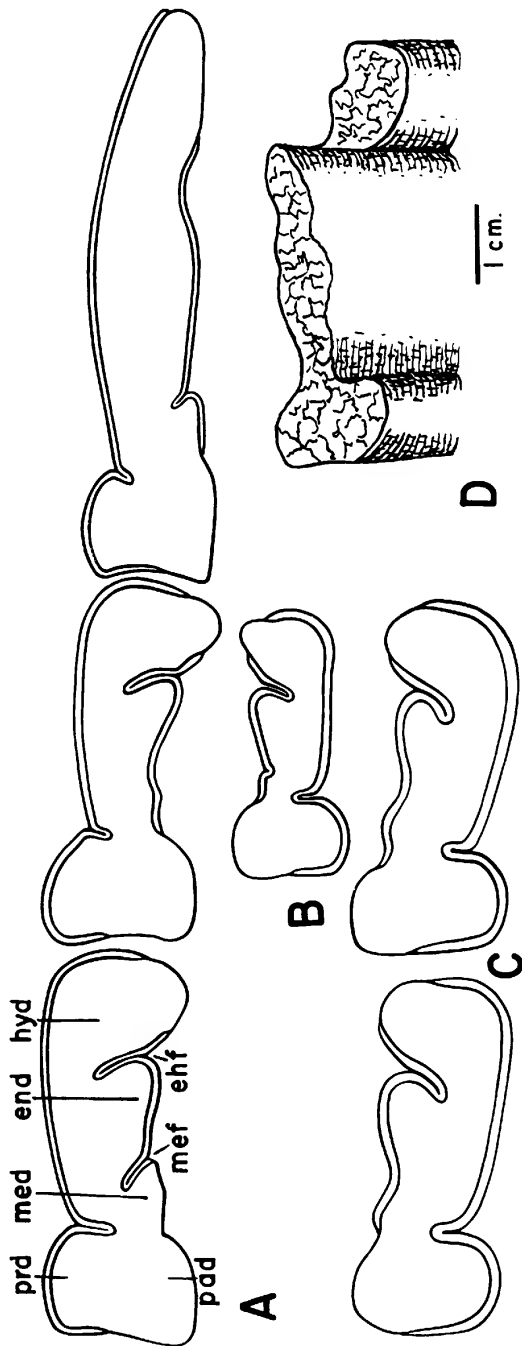


Fig. 8. A. *Mixoloxodon larensis*, paratypes, A.M.N.H. No. 48852, right M<sub>2-3</sub>; A.M.N.H. No. 48851, right M<sub>3</sub> (reversed). B. *M. larensis*, El Salvador specimen, U.C.M.P. No. V4201/37040, left M<sub>2</sub>. C. *Trigononopsis lopesi*, holotype, D.G.M. No. 55-M, left M<sub>2-3</sub>. D. *Toxodontherium imbricatum* Nectario Maria, C.L.S. specimen, right M<sub>1</sub> or M<sub>2</sub> (reversed). All figures in crown view of cross section; all  $\times 1$ . Abbreviations: ehf, ento-hypoconid fold; end, entoconid; hyd, hypoconid; med, metaconid; mef, meta-entoconid fold; pad, paraconid; prd, protoconid.



TABLE 4  
MEASUREMENTS (IN MILLIMETERS) OF LOWER MOLARS OF *Mixotoxodon larensis* AND THE NICARAGUAN *M*<sub>2</sub>

	Total Length <sup>a</sup>	Trigonid <sup>b</sup> Length by Width	Maximum Width at Metaconid	Maximum Width at Entoconid	Maximum Width of Talonid	Depth of Meta- entoconid Fold
A.M.N.H. No. 48852						
M <sub>1</sub>	48 <sup>c</sup>	13.5×19	13	15	20	4
M <sub>2</sub>	46 <sup>c</sup>	14×21	11	14	18	0
A.M.N.H. No. 48853						
M <sub>2</sub>	48?	14×20	12	15	16?	1.5?
M <sub>3</sub>	ca. 70	15×18	11	—	—	2.5
A.M.N.H. No. 48855						
M <sub>2</sub>	—	13?×21?	11?	15.5	17?	2
M <sub>3</sub>	66?	13×19	ca. 11	14	12?	2?
A.M.N.H. No. 48851, M <sub>3</sub>	71?	15.5×19	13	14	13	2?
A.M.N.H. No. 48864a, M <sub>2</sub>	47	13×19	12.5	15	19	0.5
A.M.N.H. No. 48864c, M <sub>3</sub>	47	16×19.5	14?	16	20	1.5
U.C.M.P. No. V4201/37040, M <sub>2</sub>	33 <sup>d</sup>	10×15	8.5	11	13	1
A.N.S.P. No. 12110, M <sub>2</sub> (Nicaragua)	43	14×18	13	15	16.5	3

<sup>a</sup> As in table 3.

<sup>b</sup> As in table 3.

<sup>c</sup> *Sic!*

<sup>d</sup> 34.5, measured 55 mm. rootward.

more strongly inclined forward and upward than in the other lower molars.

OTHER TOXODONTID TEETH, PROBABLY *Mixotoxodon larensis* (TABLE 5): In A.M.N.H. No. 48859, almost surely a left  $I^2$ , a horizontal (transverse) line tangent to the middle of the lingual, enamelless surface is about 40 degrees to the sagittal plane of the tooth (fig. 10C, angle a; the figure is reversed). The attrition facet cuts obliquely across the circumference of the tooth. There is a shallow, longitudinal, concave groove in the lingual surface, lying mainly to the right of the midline, and another one in the labio-lateral surface.

A.M.N.H. No. 48864h appears to be a right  $I^1$ , assuming that it is from the same species as No. 48859, and judging by the distribution of enamel. This designation also assumes that  $I^3$  is small or absent, as in other toxodontids. Shallow grooves seem to occur as in the preceding specimen, unless one is deceived by the bad state of preservation. Angle a is about 70 degrees (fig. 10B).

A.M.N.H. No. 48864i (fig. 9A) consists of most of a strongly curved tooth with one enamel band, which at first glance resembles  $P_2$  of *M. larensis*. It is more curved, however, and the position of the enamel band is different. I think it is an upper tooth, probably a left  $I^3$  or canine rather than a  $P^1$ , on the basis of the statement of Roth (1898, p. 59) that  $P^1$  of *Toxodon* has two enamel bands, both of which disappear in old age. *Toxodon* lacks  $I^3$  and C, and I do not know what the enamel situation is in other toxodontines for these three teeth.

Besides the premolar mentioned above as a probable  $P^4$  of *M. larensis* (A.M.N.H. No. 48864 l, fig. 9D), there are three other cheek teeth that make very good jaw mates for such a  $P_4$  in the same species. A.M.N.H. Nos. 48864j (left), 48864k (right), and 48864 l (right) form a believable series with one another and with A.M.N.H. No. 48864m (left) as  $P^2$ – $M^1$ , respectively (fig. 9B–E). It seems barely possible that No. 48864j could be a younger growth stage of the tooth represented by No. 48864k, as the former has the lingual enamel band less than one-third of the transverse width of the tooth, as compared with greater than one-half in No. 48864k. All the premolars are helically twisted a little—in the direction of a left-handed screw if the tooth is right, right-handed if left. The twisting is much less noticeable in No. 48864j than in the others. A.M.N.H. No. 48863b (left) is almost enough like No. 48864k to be its mate, so is likewise probably a  $P^3$ .

There are parts of four upper molars, none of which are  $M^3$ : A.M.N.H. Nos. 48860a, 48862b, 48864d, and 48864m—the last-named (fig. 9E) left, the others right. A.M.N.H. No. 48862b differs from the

rest in having the labial enamel band concave, excepting, of course, at the styles, while in the others a transverse straight line would lie tangent to the styles. A.M.N.H. No. 48860a is a little larger than the rest, but has a narrower enamel band on the protoloph and a much less conspicuous metaloph. The part exposed lingually between the two lingual pillars is about 4 mm. in No. 48860a, 7 mm. in No. 48862b, and 9 mm. in Nos. 48864d and 48864m. Also, the protocone, or anterior lingual pillar, is relatively wider and less linguad-projecting in No. 48860a. Perhaps this tooth is an M<sup>2</sup> and the others are M<sup>1</sup>. The molar fragment from Honduras is preserved only anterior to the protocone and is somewhat smaller than the corresponding part of the San Miguel teeth. It differs from the latter in having a relatively narrow, enamelless strip between the labial and anterolingual enamel bands, and a line drawn tangent to the labial styles would be convex instead of straight or concave.

TABLE 5

MEASUREMENTS (IN MILLIMETERS) OF PROBABLE *Mixotoxodon lavensis* TEETH

	Maximum Length	Maximum Width
A.M.N.H. No. 48864h, I <sup>1</sup> ?	23?	30?
A.M.N.H. No. 48859, I <sup>2</sup> ?	26?	31?
A.M.N.H. No. 48864i, I <sup>3</sup> or C <sup>sup</sup> ?	15	14
A.M.N.H. No. 48864j, P <sup>2</sup> ?	28	22
A.M.N.H. No. 48864k, P <sup>3</sup> ?	36	25
A.M.N.H. No. 48864 l, P <sup>1</sup> ?	49	29
C.N.H.M. No. P-26963, P <sup>1</sup> ?	46	28
C.N.H.M. No. P-26964, P <sup>1</sup> ?	46	29?
A.M.N.H. No. 48864d, M <sup>1</sup> ?	70	32
A.M.N.H. No. 48864m, M <sup>1</sup> ?	69	33
A.M.N.H. No. 48860a, M <sup>2</sup> ?	73?	38?

DISCUSSION: The first species that requires consideration in comparison with *Mixotoxodon lavensis* is *Toxodontherium imbricatum* Nectario Maria (1937). Hermano Nectario has very kindly sent me several drawings of *T. imbricatum* teeth, from which it is obvious that we are dealing with very different species. The total absence of the meta-entoconid fold in the lower molar of *T. imbricatum* shown in figure 8D is quite proper for a *Toxodontherium*, but is unlike the condition in the *M. lavensis* molars, all of which have that fold at least indicated by a definite concavity.

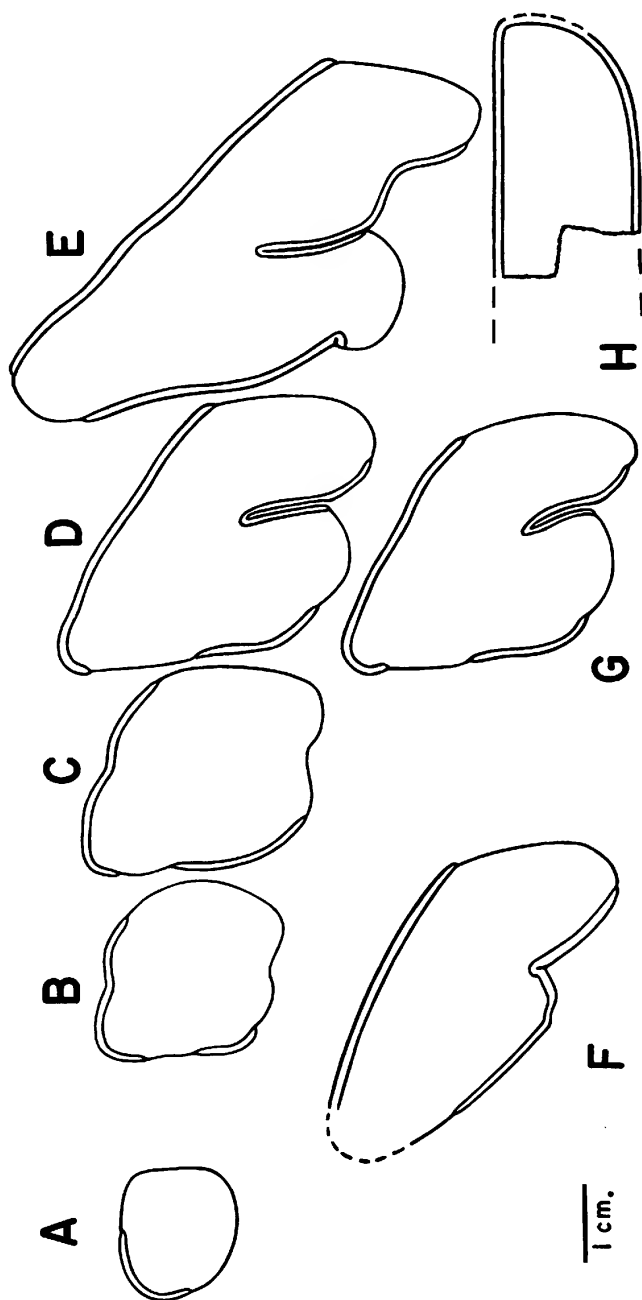


FIG. 9. A-E. Left upper toxodontid teeth from San Miguel. A. A.M.N.H. No. 48864i, probably I<sup>3</sup> or C<sup>sup</sup>. B. A.M.N.H. No. 48864j, P<sup>2</sup>?. C. A.M.N.H. No. 48864k, P<sup>2</sup>? (reversed). D. Referred to *Mixotoxodon larensis*, A.M.N.H. No. 48864 l, P<sup>2</sup>? (reversed). E. A.M.N.H. No. 48864m, M<sup>2</sup>?. F. A.M.N.H. No. 4886 l, San Miguel tooth, possibly a toxodontid premolar. G. C.N.H.M. No. P-26964, referred to *M. larensis*, Honduras specimen, same tooth as in D. H. A.M.N.H. No. 48857b, unidentified San Miguel tooth. All figures in crown view of cross section; all  $\times 1$ .

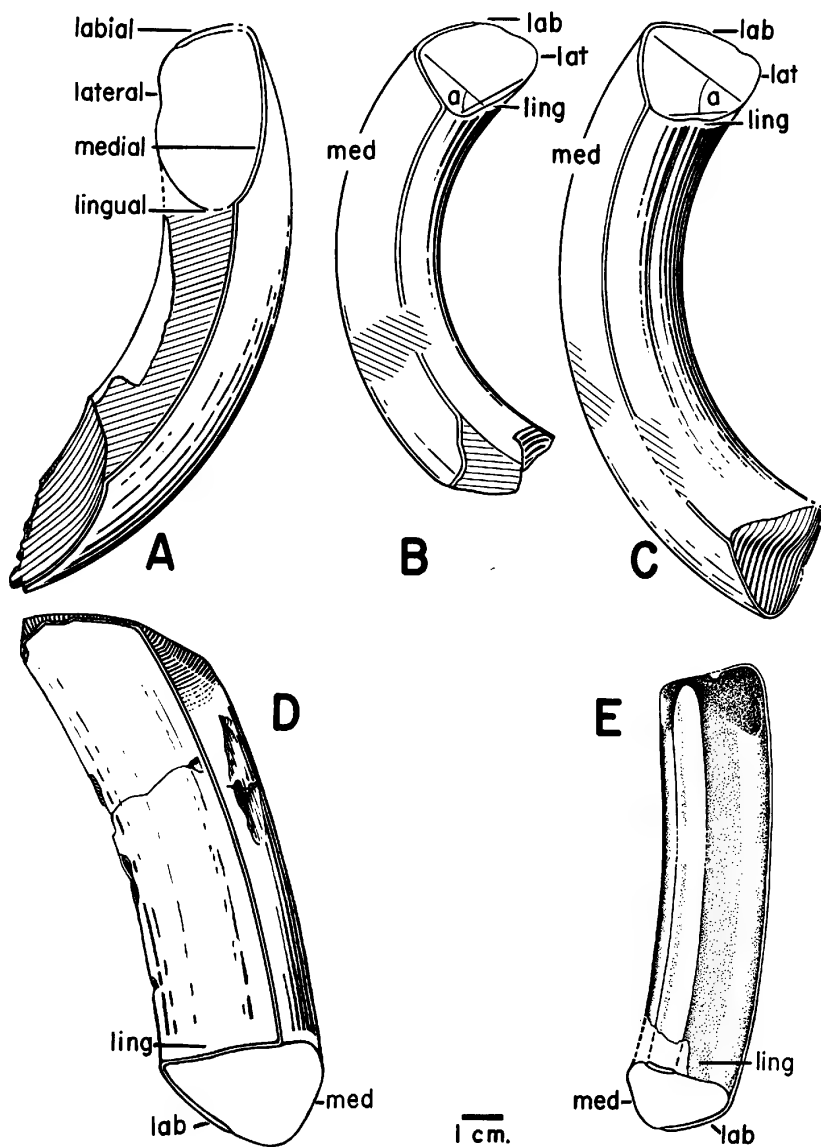


FIG. 10. Toxodontid incisors positioned so as to show maximum curvature. Occlusal ends shown with wear facets, rootward ends with true, transverse cross sections. A-D. From San Miguel. E. From Honduras. A. A.M.N.H. No. 48863a, left I<sup>2</sup>. B. A.M.N.H. No. 48864h, right(?) I<sup>2</sup>?. C. A.M.N.H. No. 48859, right(?) I<sup>2</sup>? (reversed). D. A.M.N.H. No. 48856, left I<sub>s</sub>. E. *Mixotoxodon larensis*, C.N.H.M. No. P-26969, right I<sub>s</sub>. All figures  $\times 1/2$ . Abbreviation: a, angle between lingual surface and sagittal section of tooth.

Despite the obvious differences in structure between *M. lavensis* and *Trigodonops* Kraglievich (type, *Toxodon lopesi* Roxo), from the region of the upper Juruá River, Acre, Brazil (Pliocene?), I originally intended to include the San Miguel species in *Trigodonops*, mainly by the process of elimination. But I now feel that the differences outweigh the similarities and preclude generic identity. Even the considerable individual variation in the lower cheek teeth described above does not in any way tend to decrease the dissimilarities between the two forms (cf. figs. 7A, C, 8A, C; see also Paula Couto, 1956, figs. 3–6). In fact, the more extreme variants are less like *Trigodonops* than are the paratypes.

Similar considerations prevent assignment of the San Miguel species to *Gyrinodon*<sup>1</sup> Hopwood.  $M_3$  is rather similar in both, as is the general shape of  $M_2$ . But  $M_1$  in *Gyrinodon* has a very convex labial border of

---

<sup>1</sup> The age of *Gyrinodon quassus* is at present uncertain. Both Parkinson (1928) and Halse (1938; 1947) agree that the solid beds outcropping in the region of the locality (La Puerta formation, 3 miles south of El Mene de Mauroa oil field, western Buchivacoa, Falcón, Venezuela) consist of an upper and lower part. The upper (mottled clays) is much younger than, and unconformable to, the lower one. Parkinson (1928, p. 570) feels that a "Lower to Middle Pliocene age appears most probable" for the upper beds, while Halse (1947, p. 2174) and some other later authors think that they are "possibly Pleistocene." According to Parkinson (1928, p. 570), "It was in the upper . . . beds that the bones . . . were found." Halse (1938, p. 178), however, states that "They were found . . . where rocks about half way down the La Puerta column are exposed at [the] surface, but were probably associated with a gravel deposit." "About half way down" is either in the top of the lower beds (considered Miocene by Parkinson; Mio-Pliocene by Halse; middle Miocene by Sutton, 1946; Kehrler, 1956), or the bottom of the upper beds. Parkinson (1928, pp. 570–571) mentions an "overlying superficial boulder-deposit . . . within a few score yards of the bone locality, . . . presumed to be of early Pleistocene age. As, however, the boulders must have travelled a considerable distance, it is considered that the bone fragments also would have been greatly rounded, and would not have been found only in two patches about 100 yards apart, together with Crocodilian and Chelonian remains, but would have been more scattered.

"The superficial deposits . . . consist of . . . closely aggregated . . . well-rounded boulders, from 3 feet downwards, as a rule distinctly sorted. . . . [They are] clearly older than and [do not resemble] the [underlying] sandstones." The situation is quite different from that at San Miguel, where the bone beds consist of ill-sorted pebbles derived from the underlying Cretaceous beds, and where most of the bones, though fragmented, are not worn round. They were probably deposited not far from their place of origin, along with the pebbles.

If Halse is right about where the El Mene bones were found, *Gyrinodon quassus* is certainly Pleistocene. If Parkinson is right (which seems to me a little more likely), then the age is that of the upper La Puerta beds: uncertain, but possibly Pleistocene and older than the boulder deposit.

the talonid, besides the normal distribution of enamel;  $M_2$  has two lingual enamel folds; and in all the lower molars these folds are widely open sulci in contrast to the tightly pleated ones of *Mixotoxodon*.

$M_3$  of *Stereotoxodon ameghinoi* Kraglievich (1930, fig. 3) is similar to that of *Mixotoxodon* and *Gyrinodon* in having a shallow concavity in place of the ento-hypoconid fold. A  $P_3$  attributed to *S. superbus* Kraglievich (*loc. cit.*) is similar to that of *M. larensis*, but has the labial division between the trigonid and talonid a broad concavity instead of an obtuse angle. In general the numerous teeth of several species described by Kraglievich (*ibid.*, pp. 141–145) are too different in proportions, shape, and/or distribution of enamel for identification with the San Miguel species. One noteworthy fact, however, is the specific variation in the lingual folds of the lower molars attributed to *Stereotoxodon*. He writes, “*el repliegue interno anterior [meta-entoconid fold] es tan superficial que está reducido a una simple línea*,” for a presumed  $M_2$  attributed to *S. superbus* (*ibid.*, p. 143); and similarly for  $M_{2-3}$  of *S. feruglioi* Kraglievich (*ibid.*, p. 145, footnote). If all the presumed *Stereotoxodon* teeth are correctly identified to genus, Kraglievich has given us further reason for abandoning the subfamilial distinction between the non-nesodontine toxodontids.

The type material of *Neotrigodon* Spillmann is unlike that of *Mixotoxodon*:  $P_{2-4}$  are similar in shape to  $P_2$  of *Mixotoxodon*, and  $P_4$  has lingual enamel (Spillmann, 1949, pl. 2, fig. A; Paula Couto, 1956, fig. 7A). Among several isolated teeth from Acre, Brazil, Paula Couto has described an  $M_3$  (*ibid.*, fig. 9F) similar to that of *Gyrinodon*, *Mixotoxodon*, and *Stereotoxodon*. He suggests that it may belong to *Neotrigodon*, as also another tooth identified as  $I^2$  (*ibid.*, fig. 9C). In cross-sectional view the latter strikingly resembles  $I_{1-2}$  of *M. larensis*.

On the whole it occurs to me that what is known of these various forms is sufficient to separate them taxonomically, but barely sufficient to set them in any very convincing phylogenetic arrangement. Even where they seem to have some character in common (e.g., lack of the ento-hypoconid fold in  $M_3$ ), each has its own peculiarities in most other respects. It is probably better at present to consider such features as indicating parallelism rather than relationship.

COMPARATIVE ANATOMY OF *Mixotoxodon larensis*: The lack of antieriad divergence of the mandibles is in conspicuous contrast to the splayed-out configuration in *Toxodon*, in which the borders of the jaws are divergent anterior to  $P_4$ . In *Trigodon* Ameghino and *Nesodonopsis* Roth the divergence is somewhat less than in *Toxodon*; it is still less

in *Adinotherium* Ameghino, *Nesodon* Owen, and *Xotodon*. I have not seen figures or specimens of other genera, but so far the mandible of *Mixotoxodon* is unique.<sup>1</sup>

The extension of the mandibular symphysis seems to be individually variable in toxodontids, but it is not so far posterior in the *M. larensis* specimens as in some of *Toxodon*, *Trigodon*, and *Xotodon*. In *Trigodonops* it reaches the anterior end of  $M_1$  (Paula Couto, 1956, fig. 3), about as in *Mixotoxodon*.

The various grooves and ridges on the surfaces of the teeth are described also by Hopwood (1928, p. 575) in *Gyrinodon quassus*, and I have seen them in the American Museum specimens of *Adinotherium* and *Nesodon*, and in the new Santacrucian species (Patterson and van Frank, MS). They seem to be absent where enamel is rugose, which is the case in M.C.Z. No. 9220, *Toxodon platensis*, but are present in toxodontids generally.

The position of the attrition facets of  $I_{1-2}$  on the distal end is rather unusual for a Pleistocene toxodontid. The lateral beveling in  $I_3$  is also an uncommon feature, present elsewhere apparently only in some specimens of *Toxodon burmeisteri* (Roth, 1898, figs. 26, 27). Perhaps it is an age character.

Despite all the "hodge-podge" of features displayed by various isolated molars other than the  $M_1$  fragment in the San Miguel collection, I consider them to be  $M_2$ 's of *M. larensis*, even with the El Salvador specimen measuring about two-thirds of the linear dimensions of the San Miguel  $M_2$ 's. The former is about 3.5/5.0, or 70 per cent as long anteroposteriorly as the San Miguel specimens, while according to the figures of Roth (1898, p. 71, fig. 34) in *Toxodon* the juvenile  $M_1$  and  $M_2$  there shown are at the most about 60 per cent as long as the adult ones. (If those juveniles are not *T. platensis* this figure is 50%.) Unless

---

<sup>1</sup> Although the shape of the mandible of *M. larensis* as seen in anterior view would seem to resemble that of *Toxodon platensis* in Owen's illustration (1840, pl. 5, fig. 4; refigured by Paul Couto, 1956, fig. 12), the similarity is only apparent, as the figure by itself is misleading. It is clear from Owen's text and other figures (1840, p. 30; pl. 5, figs. 1, 2) that the jaw and teeth in question are broken off through the pulp cavities. Because only the most posterior part of these teeth remains, they are of little use in comparison with crown views of other specimens. Furthermore I do not trust the distribution of enamel as shown in Owen's paper, as all the other *Toxodon* teeth (except possibly pl. 5, fig. 5) are figured and described incorrectly in this respect.

Incidentally, the isolated tooth believed by Owen to be a left  $I_1$  (*loc. cit.*) is too curved for a lower; it is much more likely a left  $I^2$ .



geographic considerations should outweigh morphological ones in this case, I believe it safe to refer the El Salvador tooth to *M. larensis*. Even though the El Salvador tooth appears different from the San Miguel  $M_2$  in figure 8, it falls well within the variation of the San Miguel  $M_2$ 's, except for the relatively wide trigonid. But this is a very variable feature. (Cf. figs. 6A, 8B.)

COMPARISON OF REMAINING, PRESUMED *M. larensis* TEETH: If the presumed  $I^2$  (A.M.N.H. No. 48859) is really from *M. larensis* the position of the wear facet, facing posteroventromedially, is in accordance with the situation in  $I_3$  of that species,<sup>1</sup> while the wear facet in A.M.N.H. No. 48863a (an isolated San Miguel tooth very similar to  $I^2$  of *Toxodon platensis*) faces posteroventrolaterally. It must be emphasized that the designations of the parts of A.M.N.H. Nos. 48859 and 48864h (fig. 10C, B) are purely hypothetical.

Among the upper premolars the one presumed to be  $P^2$  (A.M.N.H. No. 48864j) is relatively larger than  $P^2$  of *Toxodon*, but the others measure both absolutely and relatively very much as in *T. platensis* (Roth, 1898, pp. 60, 61, 64). The supposed  $P^2$  and  $P^3$  are like the  $P^2$  of *Toxodon* in having two enamel bands, and apparently like *T. elongatus* Roth in having a sulcus in the lingual side between the two lophs. This sulcus is lacking in *T. platensis* and *burmeisteri* according to Roth (*ibid.*, p. 60). The presumed  $P^4$  is like  $P^3$  and  $P^4$  of *Toxodon* in having three enamel bands and a deep lingual enamel fold. The  $P^3$ 's (?) are strikingly like the  $P^3$  (?) described by Kraglievich (1932, fig. 11) and tentatively assigned by him to *Toxodontherium listai* Kraglievich.

Through the courtesy of Prof. Bryan Patterson and the British Museum (Natural History) I have received casts of the upper dentition of *Gyrinodon quassus*.

From what I have been able to observe in toxodontids I judge that the  $P^{2-3}$  and the upper molars previously described probably do not belong to the same genus or species as *G. quassus*. More significant, however, are the differences between the San Miguel upper incisors and the upper incisor of *G. quassus*, and between the *G. quassus*  $P^4$  and the  $P^4$ 's discussed above; the implication is that the differences are at least specific and probably generic.

The (isolated) right tooth described as  $I^2$  by Hopwood (1928) is of

<sup>1</sup> Apparently toxodontids with three pairs of upper incisors have  $I^3$  reduced and situated posterior to  $I^2$ , which is therefore the lateral incisor, as indicated by the wear facet. In any case it is this tooth which occludes with  $I_3$ .

the same general plan as the  $I^1$  (?) mentioned above (fig. 10B). I should be inclined to call the *Gyrinodon* incisor a right  $I^1$  also, because the corner formed by the medial and labial sides (following the designation in fig. 10A–C) is in the most medial (sinistral) plane of the tooth. I should expect to find this corner, in an  $I^2$ , more nearly towards the middle of the tooth (compare, e.g., *Nesodon*: Scott, 1912, pls. 15, 16, and Burmeister, 1891, pl. 9, fig. 1; *Toxodon*: Burmeister, 1869, pl. 9, fig. 2; *Trigodon*: Rovereto, 1914, pl. 14, fig. 2). The very long (5 cm.), flat attrition facet is mainly in the lingual side (the side of greatest curvature, as in fig. 10B), although it actually faces a little towards the lateral side. It resembles the facet of the  $I^2$  shown by Burmeister (1891, pl. 9, fig. 1) in *Nesodon*, with the notable difference that the apex in the latter is in the sagittal plane of the tooth, but nearly sinistral in *Gyrinodon*. Further distinctions are: the *Gyrinodon* tooth has the medial-labial angle more acute; the medial-lingual angle is slightly obtuse; angle a about 90 degrees; the lateral surface narrower and protruding more laterad, forming a lip or flange; the concave groove in the labial surface deeper and much wider and centered more laterally; the labial enamel reaching to the center of this groove; a groove in the lingual side towards the medial. In curvature it is intermediate between the two San Miguel incisors.

The supposed  $P^2$  fragment of *Gyrinodon* is actually the postero-internal portion of the left  $M^1$ .

$P^3$  of *Gyrinodon* is similar in size and shape and enamel distribution to the presumed  $P^2$  from San Miguel (fig. 9B). The former is narrower and has a very shallow labial groove and a less convex posterior side. This side forms a definite obtuse angle with the labial side, quite unlike the rounded periphery of the San Miguel teeth (fig. 9B, C).

$P^4$  is smaller than the previously discussed ones. It is about 42 mm. long anteroposteriorly. As Hopwood states (1928, p. 575), the enamel fold between the protoloph and ectoloph of the *Gyrinodon*  $P^4$  is "curved away from the labial surface," so that it is much more concave lingually than in the teeth shown in figure 9D and G, and in *Toxodon*. In the *Gyrinodon* specimen only the anterior labial style is discernible.

In  $M^{1-2}$  of *Gyrinodon* the labial surface of the ectoloph has a slightly convex aspect in cross section—intermediate in this respect between the San Miguel and Honduras molars. The posterior, incurving part of the ectoloph is less conspicuous in *Gyrinodon*, and the (lingual) angle between the ectoloph and metaloph is more obtuse.

CONCLUSION: I conceive of *Mixotoxodon* as a very *Toxodon*-like animal that differs in external appearance mainly in having a cylindrical snout, instead of the quasi-hippopotamus one of *Toxodon*. In a comparison of the two genera, the snout and the narrow, closely adpressed lower incisors of *Mixotoxodon*, at present unknown to a like extent in any other toxodontid, suggest not a primitive hold-over but specialization for a different means of taking in food. Both kinds of animal must have been grazers, as both have the best kind of teeth for dealing with abrasive food. *Toxodon* has an incisor dentition somewhat recalling that of the Indian rhinoceros and may likewise have been a marshland browser and rooter. The scoop-like lower-jaw-and-teeth configuration suggests this. *Mixotoxodon*, on the contrary, has more of the character of our Recent grazers and tree-browsers in this respect; it can hardly have been a rooter, with the  $I_{1-2}$  shaped as they are and worn on the anterior end only.

#### POSTCRANIAL SKELETON

Although I have formally excluded the postcranial material from *Mixotoxodon larensis*, I think it probable that most of it belongs to that species. The radius and calcaneum certainly seem distinctive enough to prevent reference to *Toxodon*.

The axis (A.M.N.H. No. 48867) lacks the transverse processes and most of the neural spine. Such measurements as can be taken on this specimen are (in millimeters) as follows: atlas facet, total width by height, *ca.* 190 by 60; length, anterior end of odontoid process to posteroventral border of centrum, 120; height, ventral border of centrum to top of neural spine, *ca.* 175; posterior border of centrum, width by height, 77? by 100?. The posterior border of the centrum in side view is inclined forward and upward, so that the posterodorsal end of the centrum scarcely projects posterior to the neural arches. This differs from the case in the American Museum mounted cast of *Toxodon burmeisteri* (the same specimen figured by Lydekker, 1893, pl. 4, and by Roth, 1898, pl. 1) and in the mount of *T. platensis* in the Museum of Comparative Zoölogy, in both of which the posterior border of the centrum is parallel to that of the neural arches. But in A.M.N.H. No. 11172b, an axis catalogued as *Toxodon* sp. from the Pampean of Buenos Aires, the centrum is more nearly like that of the San Miguel specimen. This Pampean axis has an unusually long odontoid process.

The left radius (A.M.N.H. No. 48873; fig. 12C) measures (in milli-

meters): length, ulnar side of head to styliiform process, 332; head, depth by width, 75 by 45. It has the lateral,<sup>1</sup> i.e., scaphoid or pollical, border convex in over-all aspect, although there is a very slight concavity about 5 cm. long distal to the center of the diaphysis. On the other hand, in the *Toxodon* specimens figured by Roth (1898, figs. 50, 54, 55) and by Scott (1912, fig. 25), the lateral border is strongly concave just above the distal end. This is corroborated in the mounted specimens and in A.M.N.H. Nos. 11176, 11177, 11181, and 11182, all catalogued as Pampean *Toxodon*. But the figure of de Blainville (1864, atlas, vol. 4, *planches sans texte*, G. *Toxodon*) shows a partial specimen (proximal head missing) with the same curvature as in the San Miguel radius. Because of this curvature the styloid process and the scaphoid facet are situated medially as compared with the case in the non-Blainvillian *Toxodon* specimens. In the San Miguel radius there is a large bicipital tuberosity on the medial<sup>1</sup> or lunar side separated from the ulnar facet by a sort of collum about 1 cm. long. Diametrically opposite this tuberosity, and situated about 2 cm. distally, is another large protuberance, which I take to be the insertion of the supinator brevis muscle. Though not mentioned by Scott or Roth, such a structure can be seen in their figures: in Scott (1912, fig. 25) just below the left side (looking at the figure) of the radial head in *T. burmeisteri*; in Roth (1898, fig. 55) on the upper right side of the figure, below the head, in *T. platensis*. Slightly distal to this protuberance the proximal end of the rugose M. pronator teres ridge is situated, the ridge extending about 8 cm. along the lateral border. The various muscle scars just mentioned are present in all the specimens available to me. As in *Toxodon* and *Nesodon* there is in the San Miguel radius a small facet on the anterior<sup>1</sup> side of the head near the lateral side, for articulation with a sesamoid (Roth, 1898, fig. 54, a; fig. 53 shows this sesamoid, the *os annulare* or *hueso anular* of Roth). The San Miguel and all the *T. platensis* radii indicated above have the diaphysis curved mediad, so that more of the proximal head overhangs the lunar than the scaphoid facet—the reverse of the condition in *T. burmeisteri*. According to Roth (1898, p. 90): “la única diferencia específica parece consistir en la forma más redonda de la parte anterior en la lado interno [i.e.,

<sup>1</sup> These terms are used in accordance with general mammalian anatomy, that is they pertain to the forearm in supination. As, however, the apposed surfaces of the radius and ulna are flat and have well-developed ridges and rugosities indicating broad, strong ligamentous attachment, it is very likely that the forearm was permanently pronated as in most ungulates. Hence from a functional point of view, “medial” is interchanged with “lateral,” “anterior” with “posterior.”

medial] *de la diafisis del cúbito [sic] del T. Burmeisteri. En otros radios, que pertenecen probablemente al T. platensis, hay en esta parte una cresta.*" The San Miguel radius has such a ridge running from the bicipital tuberosity to about the middle of the bone parallel to the interosseous membrane scar laterally. The specific differences noted above are corroborated in the *Toxodon* radii that I have seen; the four isolated American Museum specimens are *platensis*-like in curvature and in the presence of the ridge.

Three of the five San Miguel ulnae (table 6) are complete: A.M.N.H. Nos. 48869 (left), 48870 (right), and 48872 (left). A.M.N.H. No. 48868 (left) lacks the olecranon and the coronoid process; A.M.N.H. No. 48871 (right) lacks the olecranon and distal head. These five bones show a great deal of individual variation. A.M.N.H. No. 48869 has a very long olecranon (which may be due in part to crushing); the distance from the free end of the olecranon to the tip of the coronoid process is a little greater than the distance from the latter to the end of the cuneiform-pisiform facet. In No. 48870 the former distance is less than the latter. The other ulnae are too broken to permit these comparisons. A.M.N.H. Nos. 48869 and 48872, as compared with the other San Miguel ulnae, have a more strongly curved sigmoid notch, so that the distance from the coronoid process to the anterior end of the olecranon just above the greater (lateral) sigmoid notch is less in No. 48869 and 48872. In the latter bone the cuneiform-pisiform facet is relatively broad and approaches a hemisphere in shape. The other specimens have this facet more nearly cylindrical. In all the San Miguel ulnae the diaphysis is quadrangular in cross section, with the medial side concave transversely. The edges of this side, below the coronoid process, are produced mediad as flanges, which become more conspicuous distally and converge upon the head. There are no obvious differences not ascribable to individual variation between the ulnae from San Miguel and those of *Toxodon* described by Roth (1898, pp. 86-87, figs. 50-52) and by Scott (1912, p. 156, fig. 25).

The one patella (A.M.N.H. No. 48874, left) measures (in millimeters): thickness at center of articular ridge, 55; mediolateral width, 130; dorsoventral height, 95. It is very much like that of *Toxodon burmeisteri* shown by Roth (1898, p. 101, fig. 65, a right patella figured upside down), and the one in the skeleton of *T. platensis* in the Museum of Comparative Zoölogy. These are somewhat different from Scott's figured specimen of a *T. burmeisteri* patella (1912, fig. 29) and A.M.N.H. No. 11187a (a Pampean *Toxodon* patella from the same col-

TABLE 6  
MEASUREMENTS (APPROXIMATE; IN MILLIMETERS) OF TOXODONTID ULNAE

	A.M.N.H. No. 48868	A.M.N.H. No. 48869	A.M.N.H. No. 48870	A.M.N.H. No. 48871	A.M.N.H. No. 48872
Middle of diaphysis, depth by width	69×56	81×57	73×56?	79×60	79×55
Length, distal end of olecranon to distal head	—	510	445	—	470?
Distance, coronoid process to distal head	330	315	315	—	310
Distance, coronoid process to distal end of olecranon	—	310	255	—	250?
Distance, <sup>a</sup> coronoid process to proximal end of olecranon	—	ca. 95	110	110	ca. 110
Width, greater sigmoid cavity	65	65	60	60	ca. 75

<sup>a</sup> Span of greater sigmoid cavity.

TABLE 7  
MEASUREMENTS (IN MILLIMETERS) OF TOXODONTID CALCANEA

	Maximum Length	Length by Width Across Sustentaculum	Maximum Height Across Ecto-fibular Ridge	Cub.	Facets, Ect.	Length by Fib.	Width <sup>a</sup> by Nav.	Sust.
San Miguel sp., A.M.N.H. No. 48865	—	ca. 105×94	63	35—	45?×35	46×27	—20?	30?×20?
Pampean <i>Toxodon</i> sp. A.M.N.H. No. 11172a	140	112×110	70	50×48?	57×40	54×40	32×17	29×25
A.M.N.H. No. 11187b	140	110×110	70	50×50	50×38	55×52?	40×20?	30×25?
A.M.N.H. No. 11187c	135	110—	70?	45×65	50×34	59×39?	43×20	37×25?
A.M.N.H. No. 11189	132	110?—	58	51×43?	53×32	49×44	24×15	—

<sup>a</sup> Maximum dimensions of facets, not including syndesmotic parts. Abbreviations as in figure 11.

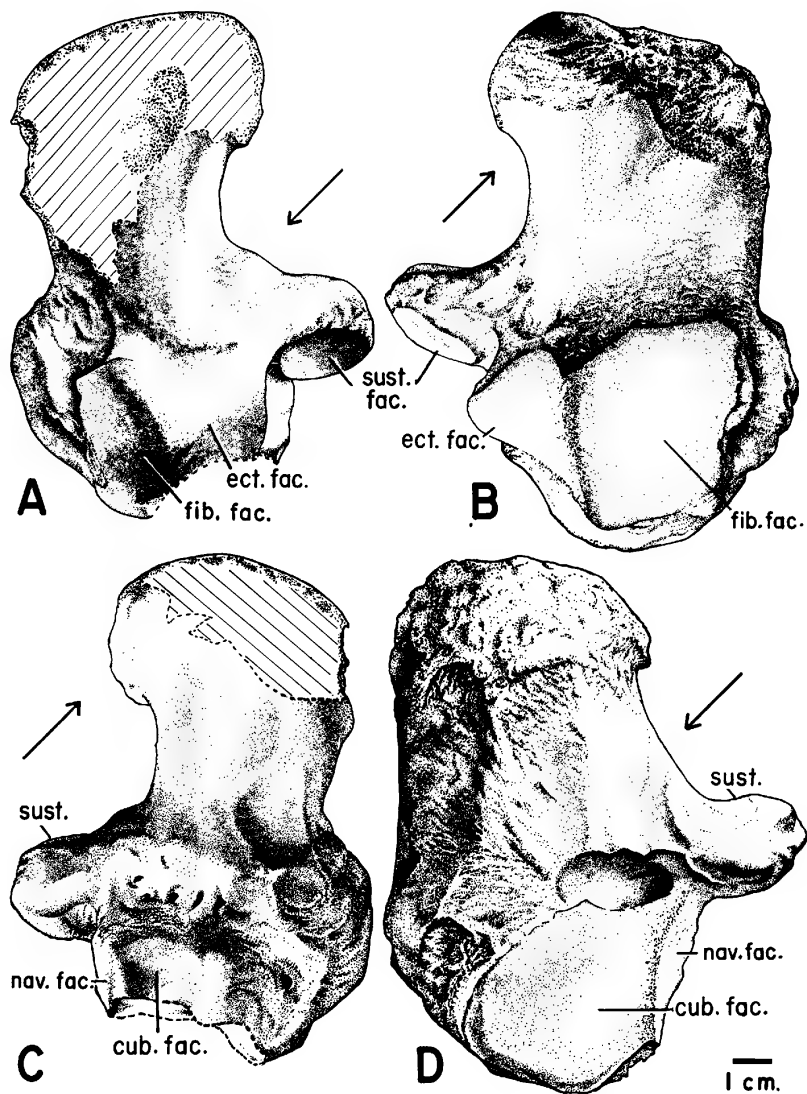


FIG. 11. A, C. A.M.N.H. No. 48865, right toxodontid calcaneum from San Miguel. B, D. A.M.N.H. No. 11187b, *Toxodon* sp., left calcaneum from Pampean of Buenos Aires. A, B. Dorsal view. C, D. Ventral view. All figures  $\times 1/2$ . Abbreviations: cub. fac., cuboid facet; ect. fac., ectal facet; fib. fac., fibular facet; nav. fac., navicular facet; sust., sustentaculum; sust. fac., sustentacular facet. The arrows indicate the direction of illumination.



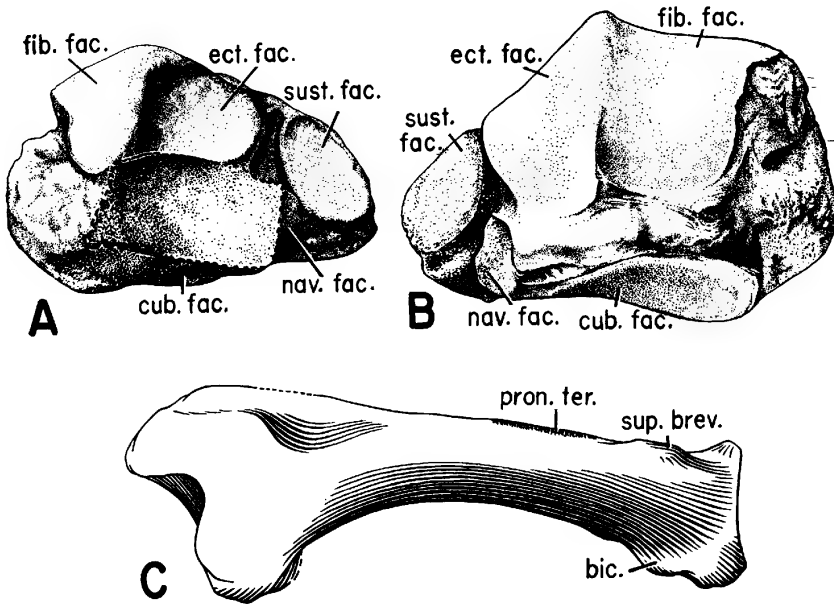


FIG. 12. A. Same as figure 11A and C, anterior view. B. Same as figure 11B and D, anterior view. C. A.M.N.H. No. 48873, left toxodontid radius from San Miguel, left lateral view. *Abbreviations:* bic., bicipital tuberosity; pron. ter., M. pronator teres rugosity; sup. brev., M. supinator brevis tuberosity.  $\times 1/4$ .

lection as the isolated axis and radii discussed above, and the calcanea discussed below). The last two are nearly symmetrical when seen from the anterior (free) side, the medial half being relatively wider than in the other specimens. Also, at least in No. 11187a, the transversely convex part of the articular surface is much broader and less like a ridge.

In the San Miguel calcaneum (A.M.N.H. No. 48865, right; figs. 11A, C, 12A; table 7) the diaphysis is trilateral in cross section, with rounded edges. Three specimens of *Toxodon* calcanea from the Argentine Pampean (table 7), namely, A.M.N.H. Nos. 11172a (right), 11187b (right), 11187c (right), and 11189 (left), have the diaphysis more or less quadrilateral. While these and the mounted specimens all have the fibular facet concave transversely, the San Miguel calcaneum has that facet convex in all directions (cf. figs. 11A, B, 12A, B). The *Toxodon* type of calcaneum is also illustrated by Burmeister (1869, pl. 11, fig. 7), Lydekker (1893, pl. 18, fig. 5), Roth (1898, fig. 70), and Scott (1912, fig. 33). In some specimens, however, the facet may be transversely convex in the anterior, vertical, part. In A.M.N.H. No. 11187c the fibular facet

is only feebly concave, but even here, as in the other *Toxodon* specimens, it meets the ectal astragular facet confluent as a hogback ridge. This is very different from the condition in the San Miguel specimen, in which the transition between the two facets is barely indicated. The sustentaculum is trilateral in cross section in this calcaneum and rather flattened and thumb-shaped in *Toxodon*. The sustentacular facet is elliptical in the San Miguel calcaneum and subcircular in *Toxodon*. Although a piece of the anterior end of the former is missing, enough remains to show that the cuboid facet is on the plantar surface, as in *Toxodon*. Unlike the case in *Toxodon*, however, it appears to have been syndesmotomic (at least laterally), and is not set off on a platform (cf. figs. 11C, D, 12A, B; Scott, 1912, fig. 33B). The cuboid and navicular facets make an angle of a little greater than 90 degrees; it is much more obtuse in *Toxodon*. A.M.N.H. No. 11187c has the cuboid and navicular facets very long and extending posteromedially onto the anterior border of the sustentaculum. In all the remaining specimens at hand (including the San Miguel calcaneum) the sustentaculum is separated from those facets by an extension of the sulcus calcanei about 1 cm. wide. In A.M.N.H. No. 11172a the fibular and ectal facets are approximately equal in their greatest widths; the fibular is wider than the ectal facet in the other *Toxodon* calcanea, while the opposite is true in the San Miguel specimen. In No. 11172a the anterior, longitudinally concave part of the ectal facet is less nearly horizontal than in the other *Toxodon* specimens. Various details of the surface are different in the several bones. The sustentaculum varies in relative size, position, and the inclinations of its surfaces; in Burmeister's illustration it is exceptionally long.

#### TOXODONTID TEETH OF UNDETERMINED IDENTITY

In the San Miguel collection there are two isolated  $I_3$ 's (A.M.N.H. Nos. 48856, left, and 48864g, right) and the  $I^2$  (No. 48863a) mentioned above, which probably represent the same species—certainly not *Mixotoxodon larensis*. The lower incisors differ from each other lingually in being weakly convex (No. 48856, fig. 10D) or weakly concave (No. 48864g). They conform closely to the  $I_3$  of *Toxodon platensis* as described by Roth (1898, pp. 65–66, fig. 26) and to M.C.Z. No. 9220, but are relatively narrow left to right. On the other hand both of them, particularly A.M.N.H. No. 48864g (concave lingually), are very much like the  $I_3$  (A.N.S.P. No. 12110, a right tooth, fig. 4B) from northern Nicaragua, described by Leidy and presumed by him to be from a

TABLE 8  
MEASUREMENTS (IN MILLIMETERS) OF TOXODONTID TEETH OF  
UNDETERMINED IDENTITY

	Maximum Length	Maximum Width	Maximum Depth
A.M.N.H. No. 48856, I <sub>3</sub>	—	41	23
A.M.N.H. No. 48864g, I <sub>3</sub>	—	43?	28?
A.N.S.P. No. 12110, I <sub>3</sub>	—	38	23
A.M.N.H. No. 48863a, I <sup>2</sup>	28	ca. 47	—
A.M.N.H. No. 48861, P <sup>sup</sup> ?	ca. 50	22	—

*Toxodon* (1886, pp. 276–277, fig. 3, erroneously designated I<sub>2</sub>). Paula Couto (1956, pp. 41–43, fig. 11B) describes a toxodontid tooth from Acre, Brazil, that strongly resembles this and the San Miguel I<sub>3</sub> in cross section. As the Brazilian tooth is a fragment, I gather that Paula Couto had to rely on Leidy's (incorrect) identification, and it is therefore understandable why he found these teeth so different from the I<sub>2</sub>'s described by Owen (1840) and Roth (1898).

The San Miguel I<sup>2</sup> (fig. 10A) seems to differ from I<sup>2</sup> of *Toxodon platensis* in the same way as the I<sub>3</sub>'s do—it is relatively narrow (although the surface of the lingual face is sheared off).

Consideration of only the intrinsic character of these incisors (including the Nicaraguan one, which may well belong to the same taxon), would lead me to think that they are from a *Toxodon* sp. close to *T. platensis*, possibly a geographic race. If, however, the lower molar described by Leidy (1866, pp. 276–277, fig. 2) along with the I<sub>3</sub> was associated with the latter, the situation is less clear. The molar (also catalogued as A.N.S.P. No. 12110) does not greatly resemble any *Toxodon* molar that I know (fig. 6B). In particular, it has very tight enamel folds, most notably the labial trigonid-talonid fold. The nearest I can match it is with the *Mixotoxodon* M<sub>2</sub>, A.M.N.H. No. 48864e. But all the San Miguel M<sub>2</sub>'s have the paraconid and hypoconid projecting more linguad and the meta-entoconid fold less deep. Leidy could not learn the exact locality of any of the Nicaraguan specimens, so the matter must wait for further, definitely associated material.

In the whole San Miguel collection nothing, not even M<sub>1</sub> of *Mixotoxodon*, is stranger than A.M.N.H. Nos. 48857a and 48861 (fig. 9F). Both of these resemble left upper premolars in general shape, size, and

helical twisting, and clearly represent the same kind of tooth. But it is inconceivable to me that they can be from the same species as the other San Miguel upper teeth. There is only a slight nick representing the lingual fold, yet the line of separation between the protoloph and metaloph is sharp, as in the presumed P<sup>4</sup> of *M. larensis*, rather than a relatively wide concavity as in P<sup>2-3</sup>. The metaloph is more robust than the protoloph, which is the reverse of the condition in the other San Miguel cheek teeth. Most fantastic of all is the distribution of enamel on the lingual side, which is completely covered with that substance except at the ends posteriorly and, apparently, anteriorly, where both specimens are broken off. In other words, the protocone, which seems to be limited anteriorly by a shallow sulcus about 0.5 cm. anterior to the lingual fold, is covered with enamel lingually—a most unusual occurrence. I can offer no useful opinion as to what sort of animal is represented by these very interesting teeth.

Finally there is A.M.N.H. No. 48857b (fig. 9H), a very fragmentary tooth. All I can say about it is that I can not match it with any tooth I know, and, by way of guessing, it may be a toxodontid incisor of some kind.

#### ACKNOWLEDGMENTS

I should like to express my sincerest thanks to the following people, who have facilitated this study: first, to Dr. George Gaylord Simpson, who suggested the undertaking and gave me full access to his field notes and the facilities of the Department of Geology and Paleontology of the American Museum of Natural History; to other members of the Museum staff, particularly Mrs. Rachel H. Nichols and Mr. Carl Sorensen, for their frequent and courteous assistance; to Prof. Bryan Patterson (Museum of Comparative Zoölogy), who has critically read the manuscript and given me the benefit of his broad and detailed knowledge; to Prof. Joseph Bequaert (Museum of Comparative Zoölogy), who identified the San Miguel snails; to Dr. Ely Mencher (Massachusetts Institute of Technology) and Dr. H. H. Renz (Mene Grande Oil Company, Caracas), for information on the geology of Venezuela; to Hermano Nectario Maria (Instituto La Salle, Caracas), for supplying information and drawings, which he has permitted me to publish, of *Toxodontherium imbricatum*; to Dr. Carlos de Paula Couto (Museu Nacional, Rio de Janeiro), for sending and permitting me to publish his figures of *Trigodonops*, and for valuable assistance during his American visit several years ago; to Dr. Horace G. Richards (Academy of Natural Sciences of Philadelphia), for the loan of the toxodontid teeth from Nicaragua; to Dr. Donald E. Savage and Dr.

R. A. Stirton (Museum of Paleontology, University of California), for the loan of the El Salvador tooth; to Mr. William Turnbull (Chicago Natural History Museum), for the loan of the Honduras teeth; to the Government of Venezuela, for making the San Miguel collection possible; to the following artists, whose work has added to the usefulness of this paper: Dr. Walter Auffenberg (University of Florida), figure 10A-D; Dr. C. de Paula Couto, figures 7C, 8C; Miss Patricia M. Washer (Museum of Comparative Zoölogy), figures 7A, B, 8A, B, 9 (all made from tracings of cross sections of plaster casts), figures 10E, 11, 12A, B; Mrs. Frances Zweifel (the American Museum of Natural History), figure 12C; and the unknown artist of the Instituto La Salle for figure 8D, sent by Hermano Nectario. Figure 2 is from a sketch by Dr. Simpson. The remaining figures were prepared by the author.

## REFERENCES

BLAINVILLE, HENRI MARIE DUCROTAY DE

1864. *Ostéographie*. Paris, 4 vols. (text), 4 vols. (atlas), issued in livraisons, 1839-1864.

BURMEISTER, HERMANN

1869. Lista de los mamíferos fósiles del terreno diluviano. *An. Mus. Pub. Buenos Aires*, vol. 1, pp. 121-470 (1864-1869).  
1891. Continuación a las adiciones al examen crítico de los mamíferos fósiles terciarios. *An. Mus. Nac. Buenos Aires*, vol. 3, pp. 401-488 (1883-1891).

HALSE, G. W.

1938. The stratigraphy of West Buchivacoa. *Bol. Geol. Min., Caracas*, vol. 1 (English ed.), pp. 175-184. [Also in Spanish, *ibid.*, vol. 1 (Spanish ed.), pp. 183-193, published in 1937.]  
1947. Oil fields of West Buchivacoa, Venezuela. *Bull. Amer. Assoc. Petrol. Geol.*, vol. 31, pp. 2170-2192.

HOPWOOD, ARTHUR TINDELL

1928. *Gyrinodon quassus*, a new genus and species of toxodont from Western Buchivacoa (Venezuela). *Quart. Jour. Geol. Soc., London*, vol. 84, pp. 573-583.

KEHRER, LOUIS

1956. Western Venezuela. In Jenks, William F. (ed.), *Handbook of South American geology*. *Mem. Geol. Soc. Amer.*, no. 65, pp. 341-349.

KRAGLIEVICH, LUCAS

1930. La formación Friaseana del río Frías, río Fénix, Laguna Blanca, etc., y su fauna de mamíferos. *Physis*, vol. 10, pp. 127-166.  
1932. Nuevos apuntes para la geología y paleontología uruguayas. *An. Mus. Hist. Nat. Montevideo*, ser. 2, vol. 3, pt. 3.

LEIDY, JOSEPH

1886. *Toxodon* and other remains from Nicaragua, C. A. *Proc. Acad. Nat. Sci. Philadelphia*, pp. 275-277.

LYDEKKER, RICHARD

1893. Contributions to a knowledge of the fossil vertebrates of Argentina.

- Part 3. A study of the extinct ungulates of Argentina. *An. Mus. La Plata, Paleont. Argentina*, vol. 2, pt. 3. (In English and Spanish.)
- MCGREW, PAUL O.  
1942. Field Museum paleontological expedition to Honduras. *Science*, vol. 96, p. 85.
- NECTARIO MARIA  
1937. Los grandes mamíferos fósiles de la región de Barquisimeto. *Bol. Geol. Min., Caracas*, vol. 1 (Spanish ed.), pp. 301-317. [English abstract, *ibid.*, vol. 1 (English ed.), pp. 283-288.]
- OWEN, RICHARD  
1840. Fossil Mammalia. In Darwin, Charles (ed.), *The zoology of the voyage of H.M.S. Beagle*. London, vol. 1, pt. 1.
- PARKINSON, JOHN  
1928. A note on the Pleistocene history of Western Buchivacoa (Venezuela). *Quart. Jour. Geol. Soc., London*, vol. 84, pp. 570-572.
- PASCUAL, ROSENDO  
1954. Adiciones a la fauna de la formación de los llanos de San Luis y su edad. *Rev. Mus. Munic. Cien. Nat. Trad. Mar del Plata*, vol. 1, pp. 113-121.
- PATTERSON, BRYAN, AND RICHARD VAN FRANK  
[MS.] A new Santacrucian toxodontid from Cape Fairweather, Patagonia.
- PAULA COUTO, CARLOS DE  
1956. Mamíferos fósseis do Cenozóico da Amazônia. *Bol. Cons. Nac. Pesquisas, Rio de Janeiro*, no. 3.
- ROTH, SANTIAGO  
1898. Catálogo de los mamíferos fósiles conservados en el Museo de La Plata. Grupo Ungulata, orden Toxodontia. *Rev. Mus. La Plata*, vol. 8, pp. 33-160.
- ROVERETO, CAYETANO  
1914. Los estratos araucanos y sus fósiles. *An. Mus. Nac. Hist. Nat. Buenos Aires*, vol. 25, pp. 1-247.
- SCOTT, WILLIAM B.  
1912. Toxodonta of the Santa Cruz beds. In Scott, W. B. (ed.), *Reports of the Princeton University expeditions to Patagonia, 1896-1899*. Princeton and Stuttgart, vol. 6, pt. 2.
- SIMPSON, GEORGE GAYLORD  
[MS.] Field notes, Venezuela, 1938-1939.
- SPILLMAN, FRANZ  
1949. Contribución a la paleontología del Peru. Una mamifaua fósil de la región del río Ucayali. *Publ. Mus. Hist. Nat. "Javier Prado," Univ. Nac. San Marcos, Lima*, vol. 1, no. 1.
- STIRTON, R. A., AND W. K. GEALEY  
1949. Reconnaissance geology and vertebrate paleontology of El Salvador, Central America. *Bull. Geol. Soc. Amer.*, vol. 60, pp. 1731-1753.
- SUTTON, F. A.  
1946. Geology of Maracaibo basin, Venezuela. *Bull. Amer. Assoc. Petrol. Geol.*, vol. 30, pp. 1621-1741.